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Old-growth Forests: Arthropods and Habitats of the H.J. Andrews Forest

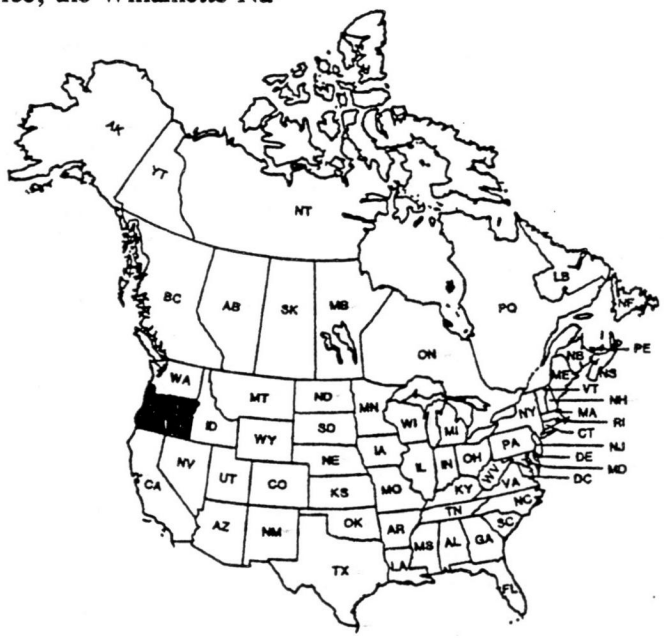
Interest in North American old-growth forests continues to increase. One of the best-studied sites is the H.J. Andrews Experimental Forest in Oregon, characterized by old-growth stands dominated by Douglas fir, true firs and other trees.

A recent report (Parsons et al. 1991*) listing 3,402 species of terrestrial arthropods from the area gives useful insights into the arthropod fauna of these forests, and excerpted here by permission from that report are summaries about some of the habitats in the forest.

The area

The H.J. Andrews Experimental Forest in the western Cascade Range of Oregon (44°14′N, 122°11′W) was established in 1948 by the USDA Forest Service. It is administered jointly by the Pacific Northwest Research Station of the Forest Service, the Willamette National Forest, and Oregon State University. The Andrews Forest covers 6400 ha (15,800 ac) and includes an entire watershed. Elevation ranges from 425 to 1620 m (1350 to 5340 ft.).

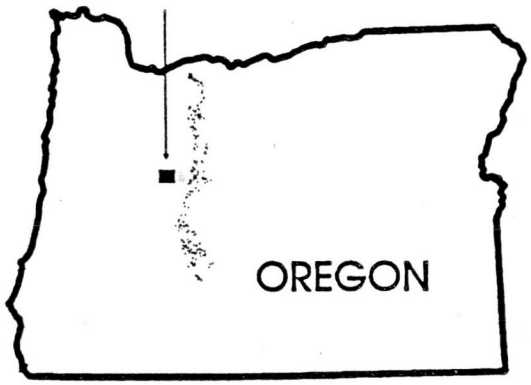
The climate is characterized by mild, wet winters and warm dry summers. Mean annual temperature is 7.9°C, with a range of -18°C to 38°C. Annual precipitation is about 230 cm (90 in.) but is seasonal, with 75 percent falling between November and March. The substantial snowpack melts quickly at elevations below 850 m but may persist above 1350 m into June. The site is typical of the mountain landscapes in the western Cascades and elsewhere in the northwestern United States, and has deep, well-drained soils. Two major forest zones are represented, the Western Hemlock Zone (300-1550 m), and the Pacific Silver Fir Zone (1050-1550 m). When designated, about 65 percent of the Andrews Forest contained



*Parsons, G.L., G. Cassis, A.R. Moldenke, J.D. Lattin, N.H. Anderson, J.C. Miller, P. Hammond, and T.D. Schowalter. 1991. Invertebrates of the H.J. Andrews Experimental Forest, western Cascade Range, Oregon. V: An annotated list of insects and other arthropods. Gen. Tech. Rep. PNW-GTR-290. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 168 p.

old-growth forest with dominant trees 400 or more years old. A substantial amount of this old-growth forest remains, along with mature stands containing dominants 140 years old, and a variety of natural stands and plantations from 1 to 40 years old. A wide range of forest phyto-associations and stream community types are represented. Although primarily forested, the area also has talus slopes, wet and dry shrub meadows, rock outcrops, and bogs. These habitats are typical of western Cascade forests. The Andrews Forest also contains 'habitat pockets' that represent a wide variety of other ecological regions.

Location of H.J. Andrews Forest



Canopy

The forest canopy provides an extensive and structurally diverse habitat for arthropods and other organisms. Various conifer species dominate the overstory, but a diverse understory occurs below. The canopy in old-growth stands may extend some 60 m above the forest floor, providing enormous surface area. Here photosynthetic rates are high, and abundant lichens are important as nitrogen fixers. Leaf surfaces, small and large twigs and branches, and the bark on the trunks all harbour distinct assemblages of organisms. In spite of chemical protection afforded by terpenes and endophytic fungi, leaves and cones are consumed by numerous herbivores. Hemlocks, Douglas-fir, and true firs share a variety of generalist feeders and their associated predators and parasitoids. Western red cedar is attacked by a limited number of specialist feeders. Defoliators have not been discovered on Pacific yew. The larvae of sawflies and moths make up much of this leaf-chewing community. Many of the more than 100 species of Geometridae found on the Andrews Forest, such as the hemlock looper, *Lambdina fiscellaria somniaria*, occur in the canopy. Aphids, some mirid bugs, leafhoppers, and thrips suck fluids from the leaves and branches. Lichens and bark fungi are fed on by springtails, oribatid mites, and bark lice. Abundant predators and parasitoids contribute to regulation of the numbers of herbivores, thus influencing their impact on the forest. Spiders such as *Metaphidippus aeneolus* are among the most abundant generalist predators in the canopy, but also present are predaceous larvae and adults of beetles, lacewings, and snakeflies. Some predatory bugs are host-plant specific; the mirid *Phytocoris nobilis* is found chiefly on noble fir. Hymenopterous and dipterous parasitoids abound, many attacking specific herbivores. Some of these parasitoids may in turn be hosts to hyperparasitoids.

Newly fallen log

A newly fallen log contains vast quantities of stored nutrients unavailable for use in the forest ecosystem until they are released through decomposition. Hundreds of species of arthropods are associated with the decomposition of fallen logs in the Andrews Forest. More than 150 different kinds of arthropods (wood feeders, predators, and parasitoids) have been found on dead and dying Douglas-fir. Some of the first insects to invade a fallen log are bark beetles, feeding on the cambium, and ambrosia beetles, such as *Trypodendron lineatum*, which burrow into the sapwood. They inoculate their initial tunnels with a diverse array of fungi, bacteria, phoretic mites, nematodes, and protozoans. A common predator of bark beetle larvae is the larva of the dolichopodid fly, *Medetera aldrichii*. After the beetle larvae are reared and the gallery is abandoned, it becomes overgrown with yeasts, bacteria, and the fruiting bodies of fungi. Fungi mobilize nutrients out of the wood and translocate them to the fruiting structures in the gallery, providing a basis for a complex ecosystem. Mi-

croarthropods, including prostigmatid and oribatid mites and springtails, feed on individual hyphae and spores. Larvae of sciarid flies and mycetophagid beetles graze on beds of fungi. Larvae of the fly *Drosophila montana* masticate fungal hyphae to promote yeast growth and then feed on the yeast. Galleries abandoned for a year contain countless nematode worms, themselves fed upon by nematophagous mites. After the nutrient-rich cambium is decomposed, log breakdown slows. Wood-boring beetles such as the cerambycid *Rhagium inquisitor* generally take several years to mature. As the larvae of these beetles tunnel deeper into the log, further access is opened for other arthropods and microrganisms. Many of these sapwood and heartwood feeders have evolved intricate symbiotic relationships with gut-inhabiting microbes for efficient conversion of the various components of the wood substrate.

Decomposed log

Conifer forests in the Pacific Northwest are characterized by the greatest quantities of coarse woody debris of any ecosystem in the world. Much of the physical degradation of logs is accomplished by a succession of arthropods associated with each advancing stage of decomposition. In the middle stages of decay, nutrients within the remaining sapwood and heartwood are often more difficult to use. Carpenter ants, such as *Camponotus modoc*, remove vast quantities of wood in constructing their nests. The dampwood termite, *Zootermopsis angusticollis*, is able to use remaining wood as a food source with the aid of symbiotic gut bacteria. In the later stages of decay, the remaining punky wood is processed into the soil system through the feeding activity of the terrestrial isopod *Ligidium gracile* and other organisms typically associated with litter decomposition. Complete decomposition may take 200 years or more. Decaying logs also offer refuge sites for small mammals, salamanders, and many other creatures that live on the forest floor. Logs in shaded old-growth forests provide a good substrate for mosses, which in turn are food for the flightless lace bug *Acalypta saundersi*. Flightlessness is a characteristic of many arthropods inhabiting old growth, as distinct from those inhabiting younger forests. For example, *Acalypta* has two common species in the Andrews Forest – *A. saundersi* in mature and old-growth forests and *A. barberi* in open sunny habitats. *A saundersi* is always flightless, but *A. barberi* is dimorphic, having both fully winged and flightless individuals. The flightless condition of *A. saundersi* appears to have developed in conjunction with long-term stability of habitat. Related flightless species of *Acalypta* in North America also have associations with habitat permanence.

Forest floor/litter

In Pacific Northwest coniferous forests, the litter layer is a seasonally renewed mixture of deciduous leaves, conifer needles, and small twigs and branches raining down from the canopy. Mosses, lichens, and fungi are abundant. This assemblage provides a stable habitat supporting a rich assortment of characteristic species of arthropods. Within the Andrews Forest, as many as 200 species per square foot of forest floor can be found. Detritivores, such as the millipede *Harpaphe haydeniana*, Collembola, and oribatid mites are very abundant, processing the litter material into humus. Because herbaceous plants are not abundant, true herbivores are scarce, although snails and slugs abound. Many root-feeding beetles, such as the weevil *Lobosoma horridum*, probably feed on both living and dead

plant material. Seeds dropping to the forest floor are eaten by lygaeid bugs and a diverse assemblage of other seed-feeding insects. Mushrooms provide food for fungivorous beetles and fly larvae. Many canopy insects use the forest floor litter layer as a pupation or overwintering site. A variety of predators, such as spiders, beetles and centipedes, occur here. The smaller forms crawl through the litter, while the larger ones patrol the surface. The large, nocturnal, flightless tiger beetle, *Omus dejeani*, wanders through the forest attacking any small arthropod it encounters. Its larval stage is hooked securely in a burrow, from which it springs out to grab passing prey. Slugs and snails are pursued by specialized snail-eating carabid beetles. *Cychrus tuberculatus*, which has an elongated head and mouthparts adapted for reaching into the narrow opening of a snail shell, is an example. These larger surface-wandering arthropods are in turn fed upon by salamanders, birds, and shrews.

Humus/soil

The humus layer is a zone of important biological activity where small pieces of litter are broken down into base nutrients by arthropods, fungi, and microbes. These nutrients percolate into the underlying soil where they are taken up by the roots of plants and returned to the canopy biomass. The humus / soil habitat is relatively uniform and stable, supporting a specialized arthropod fauna. Soil dwellers tend to be small, flightless, blind, and, in the case of springtails like *Onychiurus* sp., with reduced spring mechanisms. Individual numbers and species richness of oribatid mites and springtails are comparable to the richest soil faunas reported anywhere in the world. More than 100 species of oribatid mites, like *Nanhermannia* sp., with up to 150,000 individuals per m^2, are present in Andrews Forest soils. Some 40 species of springtails, with up to 15,000 individuals per m^2, have been recorded as well. Although most species are generally widespread, abundance is usually related to a specific stage of forest succession or a narrow range within a temperature-moisture gradient. Detritivores drive the soil ecosystem by reducing large pieces of litter into small particles readily attacked by microbes and fungi. These are then grazed by oribatid and prostigmatid mites, springtails, and a great diversity of insects. Subterranean predators include geophilomorph centipedes, pseudoscorpions, garnasid mites, and pselaphid, carabid, cantharid and staphylinid beetles, of which *Fenderia capizzii* is an example.

Clearcut

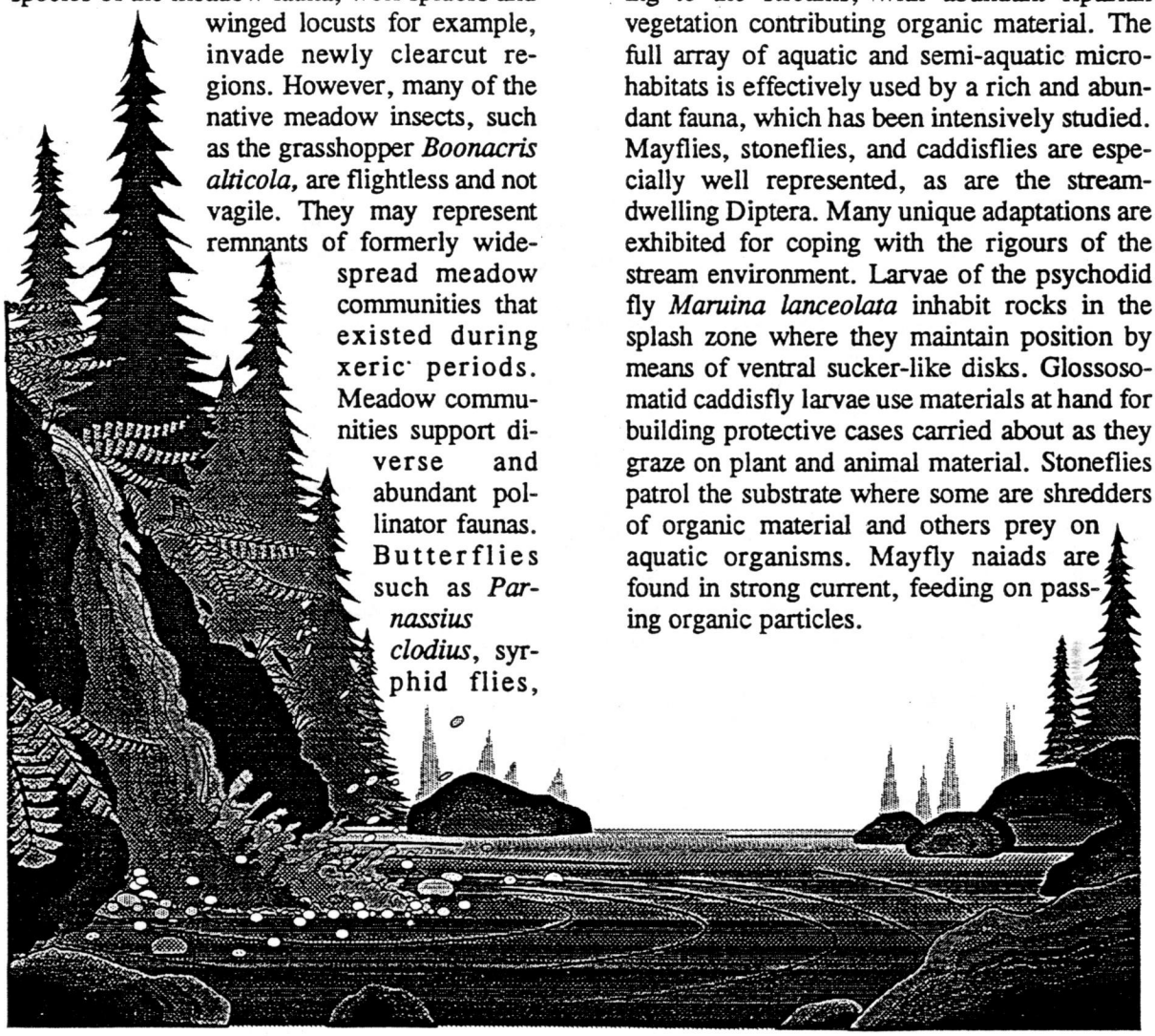
The Andrews Forest contains many small stands where, for research purposes, the trees have been cut and removed at various times over the past 40 years. These cut areas include complete clearcuts with and without the slash burned, various conifer replanting schemes, cuts with shelterwood retained for natural seeding, and selective tree removal with minimal understory disturbance. In the early stages of regrowth, annual plants and deciduous shrubs are dominant. The arthropod fauna found in clearcuts is a complex mixture of immigrants from adjacent forested land, remnants from the mature pre-logged forest, immigrants from natural meadow and forest gap communities, and some exotic species. A few species associated with forest trees can be found on seedlings as well. The diverse fauna associated with deciduous and annual plants elevates species richness to levels greater than those found in later stages of forest succession. In the early stages of regrowth, herbivores comprise a significant portion of the fauna. Most conspicuous are winged grasshoppers (not the wingless taxa common in natural meadows), sucking bugs, and caterpillars such as the larva of the noctuid moth, *Oncocnemis dunbari*. In the open, sunny, hot places typical of clearcuts, seed-feeding carabid beetles and lygaeid bugs, such as *Malezonotus obrieni*, display great species richness and abundance. The major predators in clearcuts include large carabid beetles, wandering spiders such as the wolf spider, *Schizocosa mccooki*, and ants such as *Formica neorufibarbis*.

Meadow

The few natural meadows found on the Andrews Forest are primarily at the higher elevations. They range from xeric, shallow-soil types with exposed bedrock and soil as found on ridgetops, to lush, moist, deep-soil types on hillsides. Grasses, sedges, and a variety of annual and perennial flowering plants are the predominant vegetation. Meadows are extremely rich in characteristic arthropods that are generally not shared with the forest habitat. The xeric ridgetop communities contain isolated populations of species generally characteristic of dry habitats east of the Cascade Range, of warm communities to the south, and of scrub communities in the far north. Some species of the meadow fauna, wolf spiders and winged locusts for example, invade newly clearcut regions. However, many of the native meadow insects, such as the grasshopper *Boonacris alticola,* are flightless and not vagile. They may represent remnants of formerly widespread meadow communities that existed during xeric periods. Meadow communities support diverse and abundant pollinator faunas. Butterflies such as *Parnassius clodius*, syrphid flies, bee-flies, bees, and wasps abound on flowers. Nearly all bee species are generalist foragers, as is the bumble bee *Bombus vosnesenski*. A few bee species specialize on one plant family or even a single genus of plant.

Aquatic

Aquatic habitats on the Andrews Forest are dominated by cold, clear, steep-gradient streams. Flows are typically high after fall rains and winter snow-melt, and low during the summer. Large amounts of coarse woody debris along with boulders of all sizes create a diverse habitat of riffles, falls, and pools. Substrates are mostly gravels and sands. The forest and clearcuts provide various degrees of shading to the streams, with abundant riparian vegetation contributing organic material. The full array of aquatic and semi-aquatic microhabitats is effectively used by a rich and abundant fauna, which has been intensively studied. Mayflies, stoneflies, and caddisflies are especially well represented, as are the stream-dwelling Diptera. Many unique adaptations are exhibited for coping with the rigours of the stream environment. Larvae of the psychodid fly *Maruina lanceolata* inhabit rocks in the splash zone where they maintain position by means of ventral sucker-like disks. Glossosomatid caddisfly larvae use materials at hand for building protective cases carried about as they graze on plant and animal material. Stoneflies patrol the substrate where some are shredders of organic material and others prey on aquatic organisms. Mayfly naiads are found in strong current, feeding on passing organic particles.



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